
A New Species of *Xerophyta* (Velloziaceae) from Madagascar

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ABSTRACT. *Xerophyta connata*, a distinctive new species from the mountainous northwest of Madagascar, is described and illustrated. Its morphology and anatomy are compared to those of other members of the Velloziaceae.

Among recent collections from the Manongarivo Massif in northwestern Madagascar are specimens of an undescribed member of the Velloziaceae found covering sandstone outcrops along a small river.

Xerophyta connata McPherson & van der Werff, sp. nov. TYPE: Madagascar. Antsiranana: Manongarivo Massif, E of Ankaramy, 1100 m, 14°05'S, 48°20'E, 16 Oct. 1994, *McPherson & van der Werff 16374* (holotype, MO; isotype, TAN). Figure 1.

Species madagascariensis septentrionalis antheris connatis corona evidenti inflorescentia glabra eglandulata facile distinguenda.

Plants sprawling, branched, forming a loose, tufted mat, the erect portions of the stem up to ca. 20 cm high (excluding flowers). Branches ca. 1 cm diam. at the level of the intact leaf bases, the lower portions covered by old, frayed, fibrous leaf bases. Leaves of flowering branches 8–14 cm long, 3–8 mm wide, apex acute, a curved line of disarticulation usually evident near the base, both surfaces and the margins sparsely pubescent, the pubescence somewhat scale-like at first, eventually becoming more hair-like, margin thickened and minutely denticulate, at least distally, each tooth capped by a hair or the remnants of one. Flowers 1–2(–3) together, arising from the rosette of leaves terminating each branch; pedicels 17–27 cm long, ca. 1.5 mm diam., glabrous. Perianth rotate, pink-purple with yellow at throat, deeply lobed, the hypanthial tube ca. 2 mm long, glabrous, the tepals acute, glabrous, conspicuously veined, the outer ones 18–32 mm long, 4–8 mm wide, the inner ones 19–28 mm long, 7–10.5 mm wide; corona 14–20-lobed, minutely papillose, the lobes 1–1.5 mm long, fused basally, 0.5–1.5 mm wide, obtuse or acute-acuminate apically, inserted at the rim of the hypanthial tube; stamens 6, the filaments 1–1.3 mm

long, narrowly winged and somewhat flattened, inserted slightly below the rim of the hypanthial tube and below the coronal lobes, reflexed (i.e., sloping downward into the hypanthial tube), free from one another, sub-basifixed (i.e., each filament attached to the abaxial surface of an anther very near its base but the fused anther sacs extending ca. 0.5 mm below the attachment point); anthers erect, 9–13 mm long, those opposite the outer perianth members extending 1–1.5 mm further than the others, introrse, connate into a tubular structure 3–4 mm diam.; ovary 4–5 mm long, ca. 4 mm diam., terete, glabrous, 3-locular, multiovulate; style 15–21 mm long, ca. 0.5 mm diam., the terminal 1.5–3 mm slightly thicker than the lower portion and bearing three elongate stigmatic regions; fruit unknown.

At the time it was collected, this plant was assumed to belong to the genus *Xerophyta*, the only genus of Velloziaceae reported from the island (Perrier, 1950) and one represented by many species on mainland Africa (Smith & Ayensu, 1975). Closer study revealed that the new species possesses two features that distance it somewhat from typical members of that genus. First, the anthers of the recently collected species are connate into a narrow tube, a condition apparently elsewhere unknown within the family. Second, the perianth tube bears an evident corona (sensu Jackson, 1971: “any body which intervenes between the corolla and stamens”), in this case, a lobed ring of thickened tissue at the rim of the hypanthial tube, and thus between the tepals and the stamens. Well-developed coronas had hitherto been attributed to the Brazilian genus *Barbacenia* and its close relatives but to no Old World members of this family (Perrier, 1946; Smith & Ayensu, 1976; Menezes, 1980a). In fact, the absence of a corona is given by Menezes (1980a) as one of the two features defining her version of the subfamily Vellozioidae (the other feature, that of having a single leaf vascular bundle sheath, is discussed below), which includes *Xerophyta*. However, in at least such *Xerophyta* species as *X. splendens* (Rendle) N. L. Menezes, there exist structures that may be homologous to the coronal lobes of the Madagascan collection. These ligules

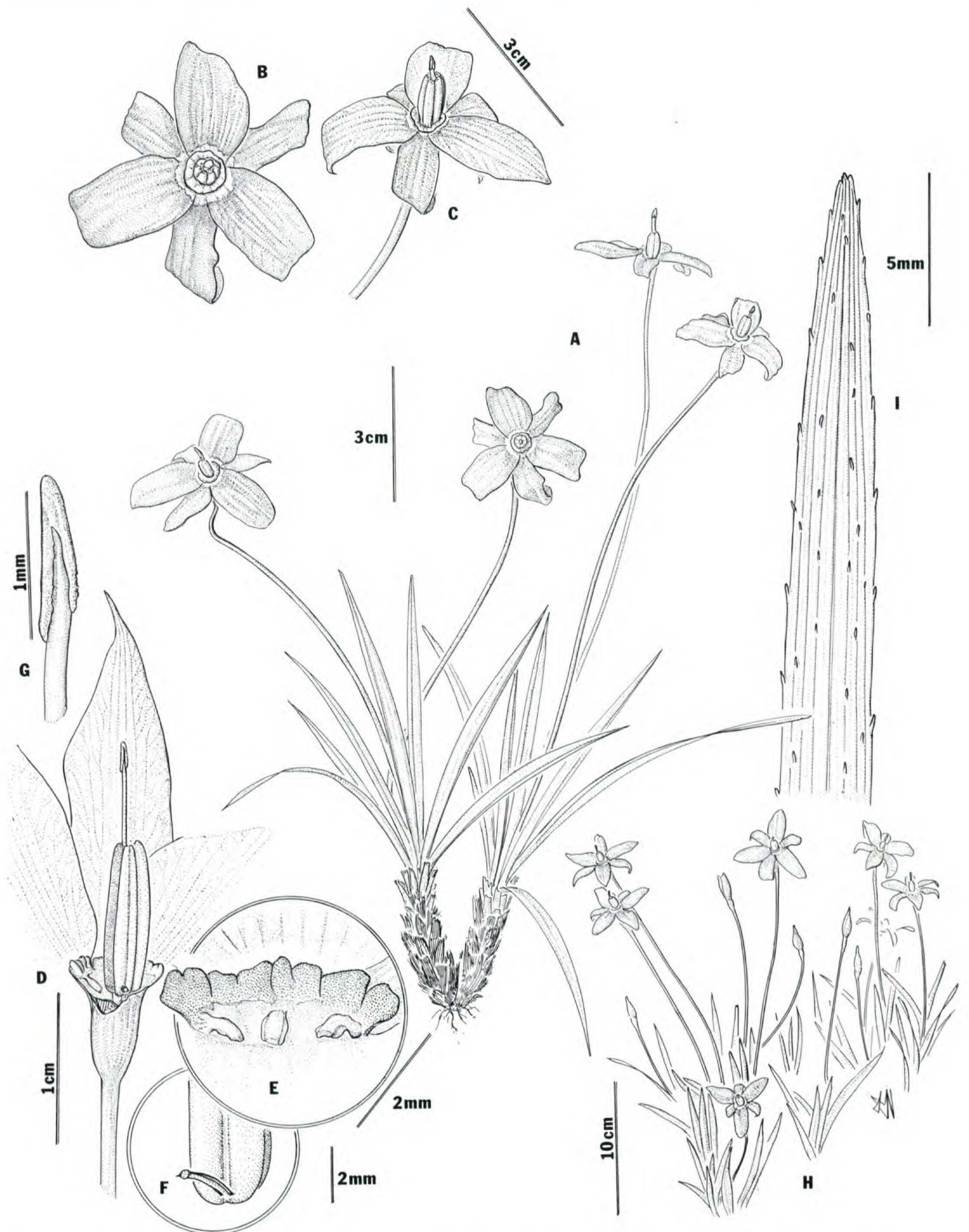


Figure 1. *Xerophyta connata* McPherson & van der Werff. —A, H. Habit. —B, C. Flowers. —D. Longitudinal section of flower, with 3 tepals, 2 stamens, and a portion of the top of the ovary removed. —E. Corona segment and 3 filaments. —F. Anther base and filament. —G. Stigma. —I. Leaf tip. (A–I, McPherson & van der Werff 16374.)

or scales, as Rendle (1894) termed them, are paired structures on the perianth tube near the bases of the sessile anthers. Coetzee et al. (1973) termed similar structures in *X. retinervis* Baker lateral ap-

pendages of the filaments, and Menezes (1980a) used *X. equisetoides* Baker as an example of an African species with filaments showing a lateral “expansion.” In our view, it is likely that the corona

Table 1. Selected characters of the three large genera in Velloziaceae. Morphological and anatomical data are based on both first-hand observations and inferences from the literature.

	<i>Vellozia</i>	<i>Barbacenia</i>	<i>Xerophyta</i>	<i>X. connata</i>
Distribution	New World	New World	Africa, Madagascar, Arabian Peninsula	Madagascar
Stamen number	(6-)9-ca. 75	6	6	6
Connate anthers	absent	absent	absent	present
Corona	absent	present	absent (1)	present
Stigma	3-lobed, capitate, peltate	capitate, small or cylindrical	cylindrical	cylindrical
Vascular bundles transcurrent	no, yes ↓ ↓	yes	yes, no ↓ ↓	yes
Adaxial sheath extension	yes, n/a	n/a	n/a, yes	n/a
Leaf bundle sheath	single	double	single or double	single
Thickened inner walls of sheath (2)	yes	no	no	no
Abaxial midvein sclerenchyma	flat, broad	thick, U-, C-shaped	flat, broad, small	flat, broad
Additional sclerenchyma	absent or strands	absent or strands	bands or strands	bands

(1) or rudimentary, see discussion.

(2) i.e., lignified vascular bundle sheath cells adjacent to phloem.

of *X. connata*, although inserted on the hypanthial tube somewhat more distally, as well as being more evenly continuous and consisting of more numerous and thicker lobes, has its evolutionary origin in structures of this kind. Its possible homology with the vascularized corona of *Barbacenia* (Menezes, 1973) remains to be determined. To conform with the recent cladistic analysis of the family (Menezes et al., 1994), the corona of *X. connata* would have to be regarded as an independent evolutionary development.

Generic limits in the family have been variously interpreted (Baker, 1875; Greves, 1921; Ayensu, 1969, 1973; Smith & Ayensu, 1974, 1976; Menezes, 1980a, b; Mello-Silva, 1991a, b; Menezes et al., 1994). Our own study leads us to agree with the view of the last-mentioned authors. Table 1 outlines the characters that led us to our generic placement for the new taxon.

ANATOMY OF *XEROPHYTA CONNATA*

Because leaf anatomical features have been used extensively in the classification of Velloziaceae (e.g., Ayensu, 1969; Menezes, 1980a), we surveyed species in several genera in order to gain insight into the relationships of *X. connata*. The results of this survey are presented in Table 2. Comments on the most informative characters are included in the discussion of leaf anatomical character states. In the Velloziaceae, features of leaf cross-sectional

anatomy are quite distinctive, often down to the species level (Ayensu, 1974). Following a description of the features of the new taxon, *X. connata*, we then attempt to determine its closest fit among the family's three largest genera.

MATERIALS AND METHODS

Dried material was available for *X. connata* and for 14 selected specimens representing other genera of the family (Appendix). Leaf specimens were restored with equal success using 5% ammonium hydroxide (Venning, 1954) or Photoflo 200/ water (1:3) (Valdes-Reyna & Hatch, 1995). Hand cross sections were made and stained two ways: in iodine-potassium iodide (1:10) and in the metachromatic dye cresyl violet acetate. Sections were placed in 30% calcium chloride, a differentiating mounting medium with a high refractive index (Keating, 1996).

OBSERVATIONS

Leaf Transverse Section. Profile: lamina flat, bent adaxially, acutely or obtusely at a small midvein. Structure: weakly dorsiventral. Thickness: 350–400 μm . Transcurrent vascular bundles regularly spaced, alternating with sets of aligned abaxial and adaxial grooves (Fig. 2B, C). Groove depth 10–30% of leaf thickness. Cuticle: birefringent, thick, smooth, following contours of the epidermal cells.

Table 2. *Xerophyta connata* and selected other specimens of Velloziaceae: leaf anatomy.

	Adax/abax grooves	Bundles trans- current	Adax sheath exten- sions	No. phloem strands	Leaf bundle sheath	Abaxial midvein sclerenchyma	Additional sclerenchyma
<i>X. connata</i>	opposite	yes	n/a	1	single	flat, wing	bands
<i>X. suaveolens</i>	opposite	yes	n/a	1	single	flat, wing	bnd, strn
<i>X. sp.</i>	opposite	yes	n/a	1	single	winged	bnd, strn
<i>X. equisetoides</i>	opposite	yes	n/a	1–7	(3)	?	bands
<i>X. dasylirioides</i>	alternate	no	yes	1–2	(5)	flat, wing	bands
<i>X. eglandulosa</i>	abax only	no	yes	2	(5)	flat, wing	bnd, strn
<i>X. pinifolia</i>	alternate	no	no	2	(5)	sm, thick U	bands
<i>X. scabrida</i>	abax only	no	yes	2	single	flat, wing, F	strands
<i>Talbotia</i>	none	no	no	2	single	thick U	no
<i>Barbacenia glauca</i>	none	yes	n/a	1	double	thick V, F	no
<i>B. stenophylla</i>	none	yes	n/a	1	double	semicirc	no
<i>Barbaceniopsis</i>	opposite	yes	n/a	2	(5)	sm semicirc	no
<i>Vellozia glauca</i>	abax only	no	yes	2	single (4)	flat, wing	strands
<i>V. ornata</i>	none	no	yes	2	single (4)	flat, wing	no
<i>Nanuza</i>	none (1)	yes (2)	n/a	2	(5)	round	bands

(1) Leaves are plicate. (2) Large bundles beneath abaxial ridges are transcurrent, other lamina bundles small, immersed. (3) Phloem partially and not consistently separated from outer sheath. (4) The single bundle sheath has lignified inner walls opposite phloem. (5) Phloem separated from outer sheath. Abbreviations: abax = abaxial side, adax = adaxial side, bnd = flat band, F = flanges, n/a = not applicable, scl = sclerenchyma, semicirc = semicircular, sm = small, strn = rounded strand, U = U-shaped, V = V-shaped.

Epidermis: cells small, cuboidal in transverse section. Stomata: on sides of abaxial grooves. Mesophyll: weak tendency toward differentiation into short palisade cells adaxially, and horizontally elongated cells abaxially (Fig. 2B, C). Air space: about 2% in spongy mesophyll. Midrib bundle very small. Lamina vascular bundles: parallel and evenly spaced, each surrounded by a single parenchymatous sheath. Xylem: a shallow or deep V with large median tracheid and several smaller ones on each side. In center of V, a 3rd vertical strand comprised of few tracheary cells occurs, as in leaves of most other genera examined. Phloem: a single U-shaped strand abaxial to the xylem (Fig. 2B, C). Sclerenchyma: fiber caps over both phloem and xylem together form a transcurrent girder, separated from the epidermal layers only by a single-layered, parenchymatous bundle sheath (Fig. 2B, C). The abaxial cap, Y-shaped on phloem side, extends with straight sides to abaxial epidermis. The adaxial (xylem) cap is an inverted Y facing xylem, extending as a centrally constricted column to the adaxial epidermis. Midvein fibers form a very small adaxial xylem cap. Abaxially, fibers form a broad band or wing, several cells deep and 3–4 vein widths laterally on each side, adjacent to the abaxial hypodermis (Fig. 2A). No flanges extend in an adaxial direction lateral to the midvein. The band is somewhat thicker in the center than laterally. In lamina,

additional fibers form subepidermal bands, 1–2 cells deep on either side of bundles, extending to edge of grooves on both surfaces (Fig. 2C). Margin: blunt V-shape with apex pointing abaxially. Triangular marginal sclerenchyma present beneath hypoderm. Leaf sheath: surface grooves absent. Non-functional mesophyll becomes large aerenchyma spaces between bundles.

DISCUSSION OF LEAF ANATOMICAL CHARACTER STATES

Grooves. These are usually deep, parallel with the linear axis of the leaf (parallel with vascular bundles), and usually occupying 10–30% of the leaf thickness. Grooves are on abaxial surface (Fig. 2D) or on both surfaces when present. Whether they are opposite or alternate along the adaxial and abaxial surfaces appears to be species specific. One surface may have grooves of a greater frequency than the other surface.

Fibrovacular bundles. Fiber strand (bundle cap) types were defined for Cyperaceae by Metcalfe and Gregory (1964) in a way that is readily adaptable to Velloziaceae as well. For lamina bundles (with the adaxial side oriented up), sclerenchyma (fiber) patterns as seen in cross section are referred to by these authors as “Y-shaped” (inverted) on the adaxial side and as “Y-shaped girders” on the ab-

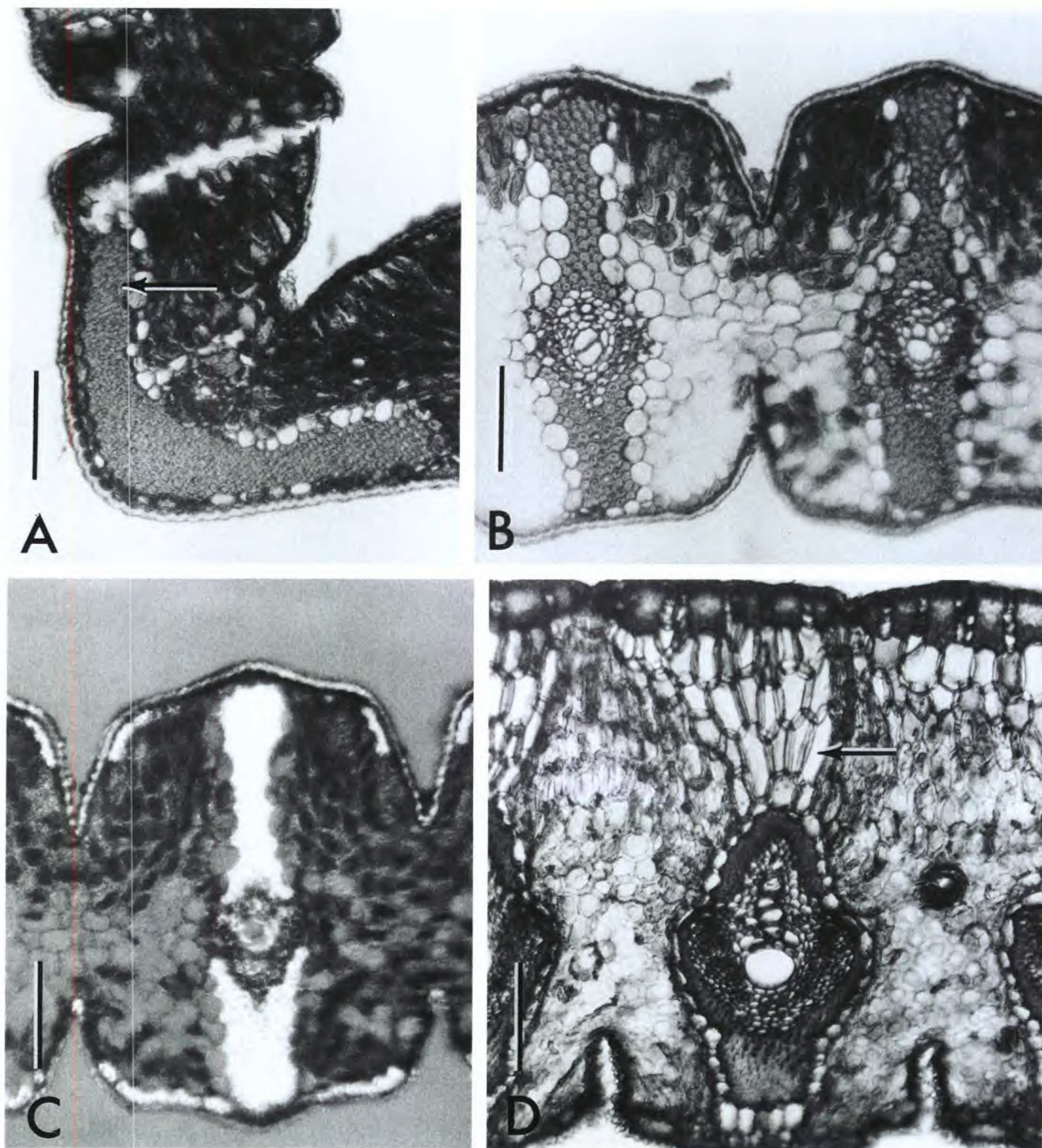


Figure 2. —A. *Xerophyta connata*. Midvein showing flat winged abaxial sclerenchyma strand (arrow). —B. *X. connata*. Non-polarized view of leaf lamina showing single sheath surrounding vascular bundle and adaxial palisade tissue. —C. *X. connata*. Polarized view showing transcurrent sclerenchyma. Note additional subepidermal strands of sclerenchyma beneath both surfaces. —D. *Vellozia glauca* Pohl. Note absence of adaxial grooves in lamina and non-transcurrent vascular bundle. Adaxial sheath extension between vascular bundle sclerenchyma and epidermis formed of a palisade-like, parenchymatous sheath extension (arrow). (A–C, McPherson & van der Werff 16374; D, Irwin 21395.) Scale lines A–D = 100 μ m.

axial side. Together, the two distinctively shaped abaxial and adaxial fiber caps cover the xylem and phloem, forming the characteristic fibrovascular bundle complex in Velloziaceae.

In many specimens examined, fibrovascular bundles are surrounded by single-layered parenchymatous sheaths. In species with transcurrent fibrovascular bundles, the fiber caps extend close to the

two epidermal layers, separated from them by only a uniseriate parenchymatous sheath (Fig. 2B, C). In non-transcurrent leaves, much of the lamina tissue adaxial to the vascular bundles is occupied by one or more tiers of aquiferous parenchyma (palisade-shaped cells) rather than by lignified fibrous tissue (Menezes, 1971). These elongated cells, without contents in restored tissue, appear to be extensions

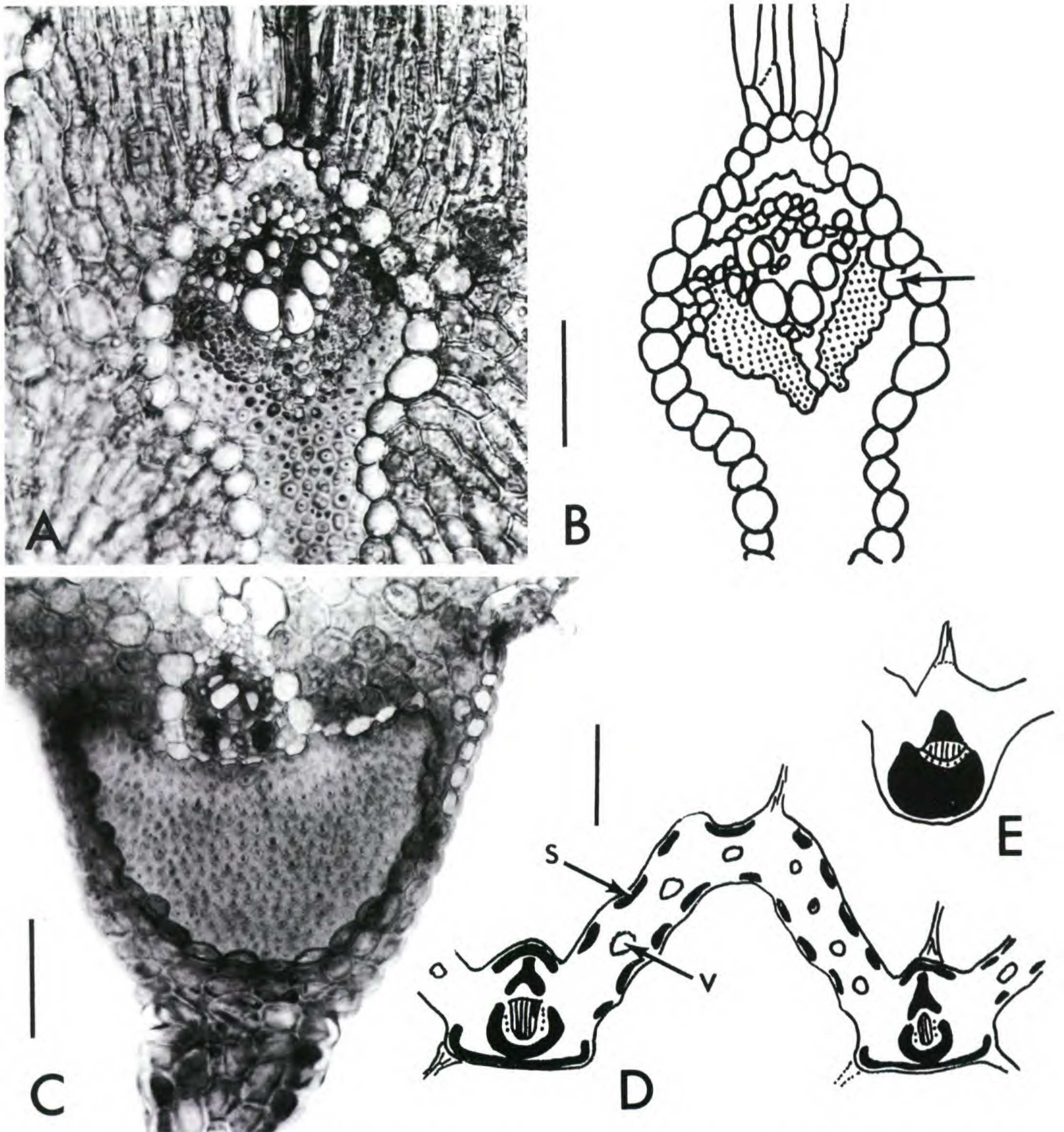


Figure 3. —A, B. *Xerophyta eglandulosa* H. Perrier. Non-transcurrent vascular bundle with parenchymatous adaxial bundle sheath extension. Cells separating phloem from bundle sheath indicated by arrow. Stippled areas represent phloem. —C. *Barbacenia stenophylla* Goethart & Henrard. Midrib showing semicircular abaxial bundle cap. —D. *Nanuza plicata* (Martius) L. B. Smith & Ayensu. Lamina cross section showing plicate structure, small laminar vascular bundles (arrow v) and subepidermal sclerenchyma (arrow s). —E. *N. plicata* midrib. Note large semicircular abaxial sclerenchyma strand. (A, B, McPherson & van der Werff 16459; C, Irwin et al. 9901; D, Davidse et al. 11823.) Scale lines A–C = 100 μ m, D–E = 200 μ m.

of the adaxial portion of the vascular bundle sheath. Beneath these parenchymatous sheaths, adaxial lignified sheath tissue is always present, forming distinctive, but smaller, adaxial bundle caps (Fig. 2D).

Midvein fibrovascular bundle. The midvein xylem and phloem strands are usually smaller than those of the main lamina veins. The sclerenchyma pattern is not usually transcurrent and is always

distinguished from that of the lamina bundles. Being much better developed on the abaxial side of the vascular bundle, the sclerenchyma usually brackets the xylem and phloem. Species with flat or tapered winged abaxial sclerenchyma bands (Fig. 2A; Table 2) do not intergrade with those with thick U-shapes (crescentiform) or semicircles (Fig. 3C, E).

Additional sclerenchyma. While in some genera or species, groups of fibers may occur only as xylem and phloem caps, others have additional subepidermal bands or rounded strands (Figs. 2C, 3D). These occur in several patterns beneath one or both surfaces.

Xylem and phloem. In Velloziaceae these tissues form a pattern most closely resembling type II bundles as defined for monocots by Cheadle and Uhl (1948). The xylem strand usually forms a V- or W-shaped structure. Abaxial to the xylem, the phloem may form a single cup-shaped strand, two distinct elliptic strands, or be cup-shaped but separated by 4–6 uniseriate, lignified partitions. This forms 5–7 functionally discrete phloem strands, although their degree of anastomosing has not been investigated.

Double bundle sheath. In single-sheathed vascular bundles (as in *Vellozia*), the parenchyma sheath is usually a single layer surrounding the entire bundle. At their most lateral extent, the xylem and phloem strands usually come in contact with this sheath. In double-sheathed vascular bundles (as in *Barbacenia*), an additional layer separates the xylem and phloem from contact with the outer main sheath (Menezes, 1980a). Menezes (1980a) used this character and a morphological character (presence of a corona, see above) to divide the family into two subfamilies, and characterized *Xerophyta* as having a single bundle sheath. However, in at least 3 of the 8 species of *Xerophyta* examined in the present study (Table 2; Fig. 3A, B) the phloem is separated from the outer sheath by what appear to be extensions of recurved xylem.

RELATIONSHIPS

Xerophyta connata differs in nearly all character states listed in Table 2 from *Vellozia*. The two have in common only the single leaf bundle sheath (partially lignified in *Vellozia*) and a flat broad midrib sclerenchyma.

Similarly, *Xerophyta connata* has little in common with *Barbacenia*. They share transcurrent vascular bundles, one phloem strand, as well as the absence of thickened inner sheath walls. These two taxa are distinguished by the presence of a double bundle sheath in *Barbacenia* and differing patterns of midvein sclerenchyma. Also, almost all *Barbacenia* species have no sclerenchyma in addition to the bundle caps (Smith & Ayensu, 1976; Mello-Silva, 1995).

While the surveyed species of *Vellozia* and *Barbacenia* have very different lists of character states, the variation we found within *Xerophyta* broadly overlaps the character states of the other two genera

(Table 2). Virtually all of the new taxon's anatomical character states are present in one or another species of *Xerophyta*. These include opposite grooves on the lamina, transcurrent bundles, some species with one phloem strand, a single bundle sheath, midvein sclerenchyma flat, winged, and possession of additional sclerenchyma as subepidermal bands. Hence the anatomical evidence supports our generic placement of the new taxon.

Anatomically, *Xerophyta connata* most closely resembles *X. equisetioides*, *X. suaveolens*, and *X. sp.* (Table 2). Of these three, the latter two seem closest on the basis of leaf anatomical evidence.

SUMMARY

Xerophyta is a highly variable genus, one ripe for monographic study. Both morphologically and anatomically the new taxon most closely resembles this sympatric genus, although within *Xerophyta* it is a very clearly marked species, easily distinguished by its connate anthers and its well-developed corona. It is also unusual in having a glabrous, eglandular inflorescence and ovary, and is the only member of its family known from northern Madagascar.

Photographs of *Xerophyta connata* can be viewed on the World Wide Web at <http://www.mobot.org/MOBOT/Madagasc/velloz.html>.

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- Appendix. Voucher specimens at MO examined anatomically.
- Barbacenia glauca* Martius ex Schultes & Schultes f., *Hatschbach* 49732, Brazil.
- Barbacenia stenophylla* Goethart & Henrard, *Irwin et al.* 9901, Brazil.
- Barbaceniopsis vargasiana* (L. B. Smith) L. B. Smith, *Vargas* 9991, Peru.
- Nanuza plicata* (Martius) L. B. Smith & Ayensu, *Davidse et al.* 11823, Brazil.
- Talbotia elegans* Balfour, *Meyer* 3342, cult: London; S. Africa.
- Vellozia glauca* Pohl, *Irwin* 21395, Brazil.
- Vellozia ornata* Martius ex Schultes & Schultes f., *Hatschbach* 51124, Brazil.
- Xerophyta connata* sp. nov., *McPherson & van der Werff* 16374, Madagascar.
- Xerophyta dasyliroides* Baker, *McPherson & van der Werff* 16482, Madagascar.
- Xerophyta eglandulosa* H. Perrier, *McPherson & van der Werff* 16459, Madagascar.
- Xerophyta equisetoides* Baker, *Plowes* 1492, Zimbabwe.
- Xerophyta pinifolia* Lamarck, *Mabberly* 1020, Madagascar.
- Xerophyta scabrida* (Pax) T. Durand & Schinz, *Balslev* 42, Tanzania.
- Xerophyta suaveolens* (Greves) N. L. Menezes, *Harder et al.* 2161, Zambia.
- Xerophyta* sp., *Harder et al.* 2077, Zambia.